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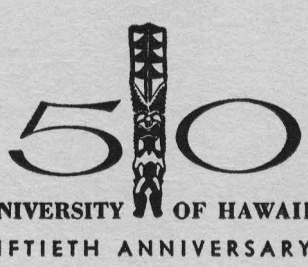

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INTRODUCTION

This investigation was initiated in 1949 to obtain pertinent information concerning the rates at which certain characters of economic importance in poultry respond to selection pressure under restricted, specified conditions. No data were available in Hawaii at that time to serve as a meter of progress and to stimulate interest in poultry breeding by local poultrymen. Aside from a few capable flock multipliers, practically all hatching eggs and chicks required for replacement purposes were imported from the mainland United States. It was reported by the Animal Industry Division of the Territorial Board of Agriculture and Forestry [Rosenberg and Tanaka (*18*)] that 1,061,820 chicks and 97,960 dozen hatching eggs were imported into Hawaii during 1949. Thus, more than a quarter million dollars were spent that year to import replacement stock. It was thought that a pedigree breeding program conducted by the University of Hawaii might create interest in local breeding and serve as a public demonstration of its worth; an effective approach, it was thought, in selling the idea that local pedigree breeding of poultry was not only a profitable enterprise but a source of savings to Hawaii's economy. For not only was money being spent annually for imported replacement stock, but the stock came from diverse breeding farms; and few, if any, of them were typical of the environmental and managemental methods employed in the Territory of Hawaii. Lush (*14*) has stressed the importance of keeping breeding stock "under the environments in which they and their descendants are intended to be used so that the desired genes may have a chance to express their effects and be recognized for selection." Under the conditions that exist on most poultry farms in Hawaii, the environment includes (1) the wire-floor system of brooding, rearing, and housing of birds, (2) small land area so that chicks are reared in close proximity to adult stock, (3) presence of numerous age groups, and (4) close proximity of poultry farms in concentrated areas. Thus, Hawaii's environment, though equable for man and his livestock, nonetheless demands adaptive genotypes for disease resistance, restricted nutrition, and wire-floor management. It was shown in a study reported by Rosenberg and Tanaka (*18*) that stock from certain good mainland breeders (all of R.O.P. caliber), in being subjected to their own specialized environments, had failed to create strains adapted to Hawaii's environment. In that study, four strains of New Hampshire chicks, hatched within 3 days

of each other, were reared and maintained under the same conditions to 17 months of age. Three of these strains were imported from the western states of the Mainland. It was found that the four strains differed significantly in growth rate, adult body weight, livability to 12 weeks of age, hen-house mortality, incidence of perosis, rate of feathering, hen-house production, monthly hen-day production, and percentage of meat and blood spots. The local strain, bred under Hawaii conditions for several generations, was outstanding for livability during both the growing and adult stages as well as in freedom from perosis. The local strain proved to be definitely superior to two of the three strains in egg production. This study suggested that chickens need to be subjected to a systematic program of selection under Hawaii conditions to increase resistance to disease(s) and perosis, and to improve egg production. The low heritability estimates reported in the literature for these characters have indicated that genic action is easily confounded by environmental interaction; and, therefore, little improvement in resistance to disease(s), wire-floor management, and aging feed in Hawaii, for example, could be bred into chickens that were reared and maintained on large, sanitary mainland poultry breeding farms where contact with disease and close proximity of mixed age groups were still avoided.

It is a widely accepted fact that pedigree breeding, involving family and progeny testing, is a potent force in changing gene frequencies for economically important characters, and the reader can find confirmatory evidence in books written by Jull (*9*), Hutt (*7*), Hays and Klein (*5*), and Lerner (*10*). But the question as to the optimum structure of the breeding flock was under attack by the population geneticists at the time this study was begun. The heritability estimates extrapolated from data obtained at widely separated land-grant universities had shown that the various characters of economic importance are not equally influenced by genes, certain characters being influenced by dominant genes, others by additive gene effects, and others, especially quantitative characters, influenced by additive gene effects that were difficult to recognize due to epistasis and dominance; and these genetic effects were obscured readily by environmental interaction. Thus, for a character like single comb, the phenotypic correlation with the genotype for comb type is very high, as is its heritability. Conversely, either egg production or livability is not only influenced by many genes (multiple factors by hypothesis) but by the environment as well, and the effect of the genotype on the total variation for these characters in the flock is very small; i.e., the heritabilities of these characters are of a very low order. To delineate its meaning, Shoffner and Sloan (*19*) defined this term as "Heritability—that fraction of the total variation associated with a characteristic which is accounted for by heredity." Because some of these estimates will be quoted under specific headings to follow, they will not be reported at this point. From such studies it followed that the system of breeding previously employed by pedigree

breeders needed to be modified to obtain maximum effectiveness. As Lush (*15*) observed, "Paradoxical though it may seem, family selection is most helpful and most needed for characteristics in which members of the family resemble each other the least; i.e., when *t* (the phenotypic correlation) is small." Conversely, family selection may actually be a hindrance to effective improvement of characters of high heritability [Lerner, *et al.* (*12*)]. Thus, the breeder whose goal is the simultaneous improvement of numerous characters not only exacts smaller shifts in the gene frequencies that affect these characters, but must, perforce, use a combination of tools; i.e., progeny testing and family records for characters of low heritability plus greater reliance on individual phenotypic selection for the characters of high heritability.

Another concept under the joint attack of certain population geneticists was the concept of average annual genetic gain in contrast with average improvement per generation. Dempster and Lerner (*2*) and Lerner and Cruden (*11*) had deduced that greater average gains might be anticipated, for egg production at least, by using a greater proportion of partially tested (record wise) cockerels and pullets. The basis for this conclusion rested on the high degree of association between the partial and complete annual egg record and on the low heritability of this trait. This concept, in turn, rested on a statistical analysis of 14 years of breeding for egg production conducted by Lerner and Hazel (*13*). From their analysis of the known selection intensities, the average interval between generations, and estimated heritability, they deduced a theoretical average gain in egg production that closely agreed with the actual gain (5.28 vs. 5.6 eggs per year). Thus a new concept in breeding for egg production was available for use when this project was begun; that is, the pattern suggested by Dempster and Lerner (*2*) in which approximately 90 percent of the females in the breeding flock consisted of pullets and 80 percent of the males consisted of cockerels.

Still another new concept was developed by the time this project had reached the family testing stage. It had been reported by Lerner, *et al.* (*12*) that for optimum genetic gains the optimum number of full sisters should vary in accordance with the degree of heritability of the character the breeder was attempting to improve. From the data shown in table 5 of their report, it may be seen that eight daughters are more desirable than lesser numbers for a character whose heritability is only 5 percent, and this relationship changes as the heritability estimate increases to the point that for a character of 70 percent heritability greater gains can be made with two sisters than with eight. Out of consideration for the then known heritabilities for egg production and livability (two characters to which we gave great emphasis) and the need to restrict family size in order to test as many families as possible within our limited facilities, it was decided that six daughters would constitute a family, and each male would be mated to six females. This decision was also influenced by a study reported by Mueller and Hutt (*16*) which had shown that 30 daughters were adequate

to progeny test a sire to differentiate resistant and susceptible families when mortality is high, whereas at least 50 daughters are needed when mortality is comparatively low. Because the hen-house mortality in our P_1 generation was 19.0 percent and there was the problem of space mentioned above, it was hoped that an average of 36 daughters per sire and 6 daughters per dam would prove to be the family unit best adapted to our circumstances for maximum genetic gain in egg production and livability.

This report will deal with the results obtained during five generations of selective breeding. It is not a final report because this study continues.

MATERIALS AND METHODS

The source of stock (P_1 generation) and its treatment have been described in detail by Rosenberg and Tanaka (*18*). Phenotypically superior cockerels and pullets were mated at 12 months of age to produce the F_1 generation. Because these birds were from four different sources (strains), it was theoretically possible to mate the breeders in 16 different combinations. Unfortunately, no males were available from stock A; and, as a consequence, only 15 of the 16 combinations of strain matings were made in approximately equal numbers. Thereafter the flock was closed and, with the exception of 6 pullets introduced during the third year of this investigation, no new stock has been added. A painstaking effort was made throughout this study to avoid the mating of collateral relatives but this was completely possible only up to and including the F_3 generation. Some inbreeding has occurred during the last two generations because it was not possible to

TABLE 1. Formulas of rations fed during the study

INGREDIENTS	RATIONS		
	Starter (pounds)	Grower (pounds)	Layer (pounds)
Ground corn	27.0	21.0	30.0
Cracked corn	0.0	20.0	0.0
Ground wheat	20.0	17.5	30.0
Whole wheat	0.0	10.0	0.0
Ground oats	10.0	0.0	19.0
Ground barley	0.0	9.0	0.0
Herring meal	5.0	4.2	5.5
Meat scrap	5.0	0.0	0.0
Soybean oil meal	26.0	12.5	9.0
Alfalfa meal	5.0	4.2	5.0
Ground oyster shell	1.0	0.5	0.0
Defluorophos	0.5	0.6	1.0
Salt	0.5	0.5	0.5
Manganese sulfate, gm.	10.0	5.0	2.5
Delsterol, gm.	10.0	10.0	30.0
Choline chloride, gm.	125.0	0.0	0.0
Fortafeed, gm.	0.0	30.0	10.0
Riboflavin, mg.	160.0	0.0	35.0

retain superior stock from sufficient ancestral males. During the selection of F_1 breeders, for example, sons of only 4 out of 15 P_1 sires were deemed worthy of use. Nonetheless, no matings have been made that were closer than first cousin matings. The number of sires and dams mated each year and the number of progeny produced may be seen in table 2. Also shown in this table is the percentage of males and females that were either partially or totally progeny tested at the time they were selected as breeders. The structure of the breeding flocks each year was patterned after the theoretically optimum plan proposed by Dempster and Lerner (2).

Realizing the importance of environmental interference on the genetic expression of the economically important characters we were subjecting to study, only three biweekly hatches were obtained each year. The first hatch was taken off each year within three days of March 3. Thus the maximum variation possible in the date of first hatch was seven days. The rations shown in table 1, fed initially to the P_1 population, were fed unchanged throughout this study, lest an improvement in response due to better rations be attributed to more desirable genic combinations. No supplements, other than water and crushed oyster shell, were fed these birds, and the day length was artificially restricted to 14.5 hours per day throughout the laying year. The starter ration was fed for 6 weeks, the grower ration was fed for 18 weeks, and the layer ration was fed to all mature fowl, including the laying pullets and breeders. Each year the first two hatches were reared

TABLE 2. Summary of breeding population used during the five generations

	GENERATIONS				
	F_1	F_2	F_3	F_4	F_5
No. of progeny tested males			2	1	1
Percent of male breeders			14.3	6.7	6.2
No. of chicks produced by these males			162	107	131
No. of partially progeny tested males		2	3	3	3
Percent of male breeders		15.4	21.4	20.0	18.8
No. of chicks produced by these males		302	340	329	408
No. of untested males	17	11	9	11	12
Percent of male breeders	100.0	84.6	64.3	73.3	75.0
No. of chicks produced by these males	1,512	1,336	1,094	975	830
No. of progeny tested females			1	3	2
Percent of female breeders			1.25	3.4	2.4
No. of chicks produced by these females			8	27	36
No. of partially progeny tested females		4	17	11	14
Percent of female breeders		5.1	21.25	12.5	16.9
No. of chicks produced by these females		31	246	159	283
No. of untested females	84	75	62	74	67
Percent of female breeders	100.0	94.9	77.5	84.1	80.7
No. of chicks produced by these females	1,512	1,607	1,342	1,225	1,050

to 3 weeks of age in Oakes electric battery brooders and then transferred to unheated grower batteries. They were moved at 6 weeks of age to open-air, wire-floor developer pens and reared there to 18 weeks of age. The third hatch was reared on litter to 6 weeks of age as described by Rosenberg and Tanaka (*17*). All pullets and potential male breeders were vaccinated against fowl pox via the wing web method at 4 weeks of age and vaccinated at 6 and 18 weeks of age with formalin inactivated Newcastle disease vaccine. When the pullets attained 18 weeks of age, a representative sample of 6 pullets from each family was housed in individual cages. As a consequence, many pullets that were superior for growth, size, and feathering were not selected once the full family complement was reached.

Because favor was shown the best developed pullets due to our interest in body size, it is more than likely that the more rapidly growing pullets in each family were selected. Thus, the data on age to sexual maturity are likely to be biased. Had there been room for more than 6 full sisters per family, this circumstance would have been avoided. Whenever possible, pullets and cockerels bearing disqualifications and defects were barred from further study.

Data were collected each year on the following characters and the records were summarized by sire and dam families:

1. Fertility
2. Hatchability
3. Chick livability to 6 and 12 weeks of age
4. Incidence of perosis
5. Feather score (rate of feathering)
6. Body weight at 6, 12, 18, and 24 weeks and 10 months of age
7. Age at sexual maturity
8. Egg production
   a. Daily egg production
   b. Meat and blood spots
   c. Soft-shell and broken eggs
   d. Double-yolk eggs
   e. Egg size during December 1 through 15
   f. Incidence of pausing and broodiness
9. Hen-house mortality

All survivors except the hens already used as breeders were marketed at the same dates each year to make room for the next generation. The birds in the first hatch were tested until July 31 of each year while those from the second and third hatches were tested until each completed thirteen 28-day periods.

These data were collected in order to provide the basis for selecting breeders inasmuch as, in the final analysis, the success or failure of a breeding program depends on the accuracy of selecting the genotypes most suited for the selector's goal. Emphasis was placed throughout this study on viability and egg production of the entire family; thus, a pullet candidate

breeder, judged on her performance to January 1, was selected, insofar as possible, from families that showed no mortality and maximum egg production averages. Those pullets whose growth rate fell in the upper quartile of the brood, and whose feathering was judged to be early, normal [refer to Jones and Hutt (8) for description], were then selected on an individual basis. Although egg size was considered, pullets were not discriminated against if their December 1 to 15 egg size averaged less than 54.0 grams. Phenotypic disassortative matings were made throughout this program with regard to egg size, balancing smaller egg size of either sire or dam against the reciprocal character of the mate. As a consequence of this procedure, little improvement in egg size was made despite its highly heritable characteristic. Cockerel candidates were selected on the basis of their sisters' records to January 1, but body size and freedom from defects and disqualifications were particularly emphasized on an individual basis.

All breeders were retained until their progenies were evaluated on the basis of their records to January 1. Dams were used again only if their progenies were superior, the number and percentage they constituted in each generation being shown in table 2. The sires were evaluated according to the total score system shown in table 3. In this instance, the decision whether a male warranted further use was based solely on the rank of that sire's earned score in comparison with the scores made by the other sires tested at the same time. Because of the low heritability estimates for viability and egg production and their great economic worth, a total of 524 out of 684 points were awarded for maximum performance. To earn 100 percent of the total score, all of the sire's progeny must survive, the daughters had to show a hen-house average of 70 eggs during the first 3 months of production, their eggs had to weigh on the average 56.7 grams during December 1 to 15, they must mature in 155 days, and average 1600

TABLE 3. Total score of sire progeny test based on heritabilities and economic worth

Character	Standard performance	Highest score	Earned score
Family viability to 18 weeks of age	100%	162	
Hen-housed viability	100%	162	
Hen-housed egg production during first 3 months	70 eggs	200	
Days to sexual maturity	155 days	10	
Egg weight ($\bar{x}$ Dec. 1–15)	56.7 gm.	25	
Average body weight at 12 weeks of age	1600 gm.	25	
Hatchability	100%	50	
Incidence of perosis	0	50	
Total score		684	

grams in body weight at 12 weeks of age. Points were also awarded for comparative freedom from perosis and percentage hatchability. It should be noted that comparatively low point awards were made for egg size and body size despite their great economic importance. Due to the high heritability estimates published for these characters, it was thought that individual phenotypic selection, following family selection for livability and egg production, would be adequate to improve these traits.

RESULTS AND DISCUSSION

Fertility

Because various methods were employed to produce fertile eggs, the results shown in table 4 for this character are not comparable. The P_1 generation was produced by floor matings, the F_3 generation by stud matings, and the F_1, F_2, F_4, and F_5 generations by means of artificial insemination. This variation in techniques was not a matter of choice or an indication of desirability. Nonetheless, the data show that it was possible to obtain 91.8 percent fertility of all eggs set during the F_5 generation. From this, it may be concluded that the lower fertility rates recorded during the F_1—F_4 generations were the consequence of technique rather than to genetic regression for this character. Five generations of breeding within a closed flock did not result in a serious depression of this trait.

Hatchability

Little change occurred in this character during the course of the investigation. As may be seen in table 4, the average rate for the P_1 generation was 78.1 percent, and five generations later 84.7 percent of all fertile eggs hatched. Had this study been summarized at the end of the F_4 generation,

TABLE 4. Summary of certain characters observed during this study

CHARACTER	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Fertility, %*	96.0	79.3	81.3	82.6	82.0	91.8
Hatchability, %	78.1	87.7	84.6	83.0	81.2	84.7
Perosis, %	3.3	3.5	4.1	2.9	2.9	3.7
Mortality to 6 weeks of age, %	1.2	2.5	2.2	2.4	1.4	0.8
All losses to 12 weeks of age, %†	8.1	15.2	4.8	5.7	5.4	5.5
Early, normal feathering, %	68.4	83.4	96.0	89.2	94.9	99.0
Hen-house mortality, %	19.0	27.0	7.2	10.1	9.0	8.4
Broodiness, %	0.0	4.0	15.3	5.0	30.0	14.0
Average number of pauses per bird housed	1.8	2.1	1.7	1.9	1.4	1.3
Average clutch size, eggs	2.3	2.9	2.8	2.9	3.2	2.8

*F_1, F_2, F_4, and F_5 generations produced by means of artificial insemination. F_3 produced by stud mating. P_1 produced by floor mating.
†These values include all perotic birds.

one might have been tempted to ascribe heterosis as being responsible for the improved rate of hatchability in the F_1 generation and a gradual regression during the ensuing years due to genetic decay. But the data obtained from the F_5 generation argue against the theory of genetic decay resulting from the gradual increase of undesirable recessive alleles. Actually, little selection pressure was exerted against this character inasmuch as the majority of the matings involved untested cockerels and pullets; and, quite often, partially progeny tested sires and dams were used whose hatchability records were not superior but because of their outstanding performance in other characters. Nonetheless, it is noteworthy that this character remained essentially the same over a period of five generations under such conditions as (1) a closed flock, (2) small annual population, (3) pullet × cockerel matings primarily, and (4) little selective pressure exerted for high hatchability. That this character did not regress may be explained by the fact that inbreeding was avoided insofar as possible when the choice of matings was consummated. Thus, from these data it may be concluded that it is possible to maintain hatchability at a satisfactory plateau within a small, restricted population, at least under the condition that the initial gene frequency for hatchability was neither outstandingly good nor bad.

Growth rate

(a) To 6 weeks of age:

Cockerels. The average body weights of the cockerel chicks at 42 days of age may be seen in table 5. This character was definitely improved by the simple process of selecting from each dam family the heavier cockerels at 6 weeks of age, provided they were free of defects and disqualifications at that age. That this simple method of selection should be so successful falls within genetic expectation inasmuch as this character has been reported to be highly heritable. Estimates of heritability of 8-week weights ranging from 0.35 to 0.50 have been reported by Fagan (*3*), 0.33 by Hurry and Nordskog (*6*), and 0.40 to 0.46 by Wyatt (*21*). Following five generations of selection, a highly significant increase in body weight resulted ($P<0.01$). The cockerels of the F_5 generation were 0.34 pound heavier at 6 weeks of age, on the average, than those of the P_1 generation. Not only was the

TABLE 5. Cockerel body weights at 6 weeks of age

CHARACTERISTIC	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Number	432	810	753	809	427	512
Average body weight, gm.	619.8	672.0	749.8	706.0	737.9	776.0
Standard deviation, gm.	97.1	93.7	69.4	77.8	70.6	80.1
Coefficient of variation, %	15.7	13.9	9.3	11.0	9.6	10.3

Between generations: $F=252.11$; $P<0.01$; L.S.D.$=\pm 9.15$ gm.; H.S.D.$=\pm 12.04$ gm.

TABLE 6. Pullet body weights at 6 weeks of age*

CHARACTERISTIC	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Number	403	715	817	748	450	510
Average body weight, gm.	544.9	587.4	611.4	611.5	631.8	659.1
Standard deviation, gm.	76.1	72.0	72.3	58.4	62.4	68.6
Coefficient of variation, %	14.0	12.2	11.8	9.6	9.9	10.4

Between generations: $F=153.91$; $P<0.01$; L.S.D.$=\pm 7.64$ gm.; H.S.D.$=\pm 10.06$ gm.

*All pullets hatched each year and alive at 6 weeks of age.

average body weight increased by selection pressure but the variations in the range of body weights were also reduced. As may be seen in table 5, the coefficient of variation was 10.3 percent for the F_5 generation as compared to 15.7 percent for the P_1 generation and 13.9 percent for the F_1 generation. It is possible, therefore, to increase body weight and at the same time attain a somewhat uniform population simply by phenotypic selection of the breeders.

Pullets. The average weights of the pullets at 42 days of age showed the same trend as those of the cockerels. As may be seen in table 6, the average weight was increased 0.25 pound after five generations of selection; this difference was also statistically significant ($P<0.01$). The variation in body weights of the pullets among the different generations was similar both in trend and percentage as those reported for cockerels to 6 weeks of age. This similarity in the coefficients of variation of both cockerel and pullet body weights indicated that up to 6 weeks of age neither sex varied more or less than the other.

(b) To 12, 18, and 24 weeks, and 10 months of age:

Due to the limitation of housing space, only the heavier cockerels (either two or three) from each dam family were selected each year at 6 weeks of age. Consequently, there were no representative samples of body weights for males at 12, 18, and 24 weeks, and at 10 months of age.

TABLE 7. Pullet body weights at 12 weeks of age*

CHARACTERISTIC	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Number	376	613	767	500	430	468
Average body weight, gm.	1361.2	1383.8	1441.4	1441.4	1442.5	1521.0
Standard deviation, gm.	136.4	112.0	132.9	117.9	139.1	134.6
Coefficient of variation, %	10.0	8.1	9.2	8.2	9.6	8.8

Between generations: $F=86.59$; $P<0.01$; L.S.D.$=\pm 14.19$ gm.; H.S.D.$=\pm 18.68$ gm.

*All pullets hatched each year and alive at 12 weeks of age.

TABLE 8. Pullet body weights at 18 weeks of age*

CHARACTERISTIC	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Number	354	Unavailable	683	413	420	449
Average body weight, gm.	1928.3	Unavailable	2048.8	2139.2	2052.6	2142.4
Standard deviation, gm.	175.9	Unavailable	209.2	182.9	194.6	213.8
Coefficient of variation, %	9.1	Unavailable	10.2	8.6	9.5	10.0

*All pullets hatched each year and alive at 18 weeks of age.

The average body weights of the unselected pullets at 12 and 18 weeks of age are shown in tables 7 and 8 and those of the selected pullets at 24 weeks and 10 months of age are shown in tables 9 and 10, respectively. At 12 weeks of age, the pullets in the F_5 generation weighed, on the average, 0.35 pound more than those in the P_1 generation. At 18 weeks of age, the pullets in the F_5 generation were, on the average, 0.47 pound heavier than those in the P_1 generation; at 24 weeks there was an increase of 0.52 pound; and at 10 months of age the increase was 1.02 pounds. These increases of the F_5 generation over the P_1 generation, except that at 18 weeks of age, were statistically significant ($P<0.01$). The weights at 18 weeks of age were not analyzed statistically because individual body weights of the F_1 generation were not available.

TABLE 9. Pullet body weights at 24 weeks of age

CHARACTERISTIC	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Number	351	411	428	393	228	302
Average body weight, gm.	2363.5	2472.3	2540.4	2617.9	2503.7	2600.9
Standard deviation, gm.	Unavailable	355.4	217.4	239.0	298.2	272.3
Coefficient of variation, %	Unavailable	14.4	8.6	9.1	11.9	10.5

Between generations: $F=17.94$; $P<0.01$; L.S.D.$=\pm 41.4$ gm.; H.S.D.$=\pm 54.6$ gm.

TABLE 10. Pullet body weights at 10 months of age

CHARACTERISTIC	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Number	278	370	418	375	362	373
Average body weight, gm.	2619.1	2764.2	2784.6	2868.0	2937.8	3083.7
Standard deviation, gm.	384.0	338.1	295.4	326.9	371.4	313.5
Coefficient of variation, %	14.7	12.2	10.6	11.4	12.6	10.2

Between generations: $F=75.26$; $P<0.01$; L.S.D.$=\pm 147.0$ gm.; H.S.D.$=\pm 193.4$ gm.

Perosis

The incidence of perosis at 6 weeks of age for each of the six generations is shown in table 4. The greatest difference between any two generations was 1.2 percent, the highest incidence occurring in the F_2 generation and the lowest in both the F_3 and F_4 generations. Despite efforts to exclude all birds from families showing a high incidence of perosis as breeders, no apparent improvement was noted. However, it is quite possible that there was a certain amount of genetic gain, but the expression of this gain may have been masked by certain environmental factors. One of these factors may have been the inadequacy of the starter ration to meet the requirements of the faster growing chicks to prevent the perotic condition. This fact is clearly shown in table 11, where a comparison of the incidence of perosis in chicks reared on wire and litter is shown. It was mentioned earlier that the first and second hatches of each generation were reared in battery brooders and grower units while the third hatch was reared on litter for 6 weeks. The incidence in each generation was higher among the chicks reared on wire than those reared on litter, and the differences between the two groups increased with each succeeding generation. Obviously, the chicks on the floor received certain benefits from the litter which supplied additional nutrients while those on the wire-floor batteries did not.

Crooked toe

In table 11 is also shown the comparison of the incidence of crooked toe in chicks reared on wire and litter. While the evidence is not conclusive, crooked toe was more prevalent among chicks reared on litter.

Rate of feathering

All chicks in this study were scored for feathering at 14 days of age to identify the different phenotypes. The system of classification shown in table 12 was based on descriptions given by Jones and Hutt (*8*) and Warren (*20*). No detailed description of each classification is included in this report because an excellent summary on the inheritance of rate of feathering and descriptions of the associated phenotypes has been given by Hutt (*7*). The classifications called "slow, retarded" or "slow, tardy" feathering

TABLE 11. Effect of management on incidence of perosis and crooked toe among chicks of comparable breeding

	PEROSIS		CROOKED TOE	
	Wire	Litter	Wire	Litter
	(%)	(%)	(%)	(%)
1952	3.6	2.4	5.5	3.9
1953	2.3	0.2	4.0	25.4
1954	3.7	0.4	12.3	33.9
1955	4.5	1.0	8.9	8.1

included chicks that had practically no primary or secondary flight feather development and no shoulder and tail feathers.

In the P_1 generation 83.5 percent showed the recessive sex-linked gene for rapid feathering (*k*), 83.6 percent in the F_1, 99.2 percent in the F_2, and 100.0 percent in the F_3, F_4, and F_5 generations. Chicks with the dominant autosomal gene for normal feathering (T) were as follows: 94.2 percent in the P_1; 93.8 percent in the F_1; 97.1 percent in the F_2; 93.4 percent in the F_3; 95.9 percent in the F_4; and 100.0 percent in the F_5 generation. The percentage with rapid, normal genotypes [(kx kx T-) or (kx Y T-)] was as follows: P_1, 78.2; F_1, 80.4; F_2, 96.4; F_3, 93.4; F_4, 95.9; and F_5, 100.0.

Although poor rate of feathering can be influenced by protein-deficient diets [Gericke and Platt (*4*)] and diets deficient in folic acid [Briggs, *et al.* (*1*)], this study has shown that this character is controlled by genes with high penetrance. After three selected generations, the sex-linked gene for slow feathering was entirely eliminated from the population. The autosomal dominant gene for normal feathering, however, was more difficult to establish. In the F_4, for instance, 4.1 percent still showed the retarded phenotype, but none showed it in the F_5 generation.

Age at sexual maturity

The average age at sexual maturity for the six generations is shown in table 13. There was no significant difference among the generations; but age to sexual maturity was lowered from 161.4 days in the P_1 to 150.0 days in the F_5. Although no rigid selection was exercised for this character, this decrease in the average age to sexual maturity was probably the result of selecting the earlier maturing pullets. Perhaps a certain amount of bias resulted from this method, but because of the limited number of cages available and the fear of losing valuable egg data and actual maturing date,

TABLE 12. Feather score of the six generations at 14 days of age

FEATHER SCORE (PERCENT)	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Rapid,* normal†	74.3	77.2	95.5	89.8	94.8	99.0
Rapid, normal with slight indentation of secondaries	3.9	3.2	0.9	3.6	1.1	1.0
Rapid, retarded	0.1	3.2	2.8	6.5	4.1	0.0
Rapid, tardy	5.2	0.0	0.0	0.1	0.0	0.0
Slow, normal	15.8	12.1	0.7	0.0	0.0	0.0
Slow, normal with slight indentation of secondaries	0.2	1.3	0.0	0.0	0.0	0.0
Slow, retarded or tardy	0.5	3.0	0.1	0.0	0.0	0.0

*Rapid vs. slow—sex-linked alleles reported by Warren (*19*).
†Normal, retarded, and tardy—multiple alleles described by Jones and Hutt (*15*).

TABLE 13. Number of days to sexual maturity

CHARACTERISTIC	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Number	313	173	150	150	155	163
Age at sexual maturity, days	161.4	162.6	154.0	160.2	156.0	150.0
Standard deviation, days	14.6	11.2	17.7	19.8	15.6	21.6
Coefficient of variation, %	9.0	6.9	11.5	12.4	10.0	14.4

Between generations: $F=1.59$; $P>0.05$; L.S.D.$=\pm 10.80$ days.

the early maturing pullets had to be housed sooner than the others. As a direct consequence, the later maturing pullets were eliminated from the laying phase of this study.

Egg weight

The average egg weights for the different generations in this study are shown in table 14. Except for the P_1 and F_1 generations when the averages were obtained from the eggs laid during the first three days in December, the averages for the other generations were obtained from eggs produced during the first 15 days of December. Jull (9) reported that the average obtained from the eggs laid during the first 10 days of the fifth month of production was a good criterion for measuring annual egg size and December was the fifth month of production in this investigation.

No definite gains were obtained for this character in this study. This was brought about by the fact that it was very difficult to select satisfactory breeder candidates which produced large eggs while possessing other desirable economic traits. As a consequence, pullets that produced small eggs but were superior in other traits were mated to cockerels or cocks whose dams, daughters, and sisters produced large eggs in order to keep a reserve of large egg size genes in the flock. This character being highly heritable could be rapidly improved in later generations by individual phenotypic selection. Furthermore, there was no economic incentive to produce extremely large eggs.

TABLE 14. Average egg weights during December 1–15

CHARACTERISTIC	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Number of birds	261	143	138	137	148	146
Average egg weight, gm.	56.80	57.80	56.48	57.14	57.20	57.25
Standard deviation, gm.	4.31	4.90	3.66	3.34	4.05	3.43
Coefficient of variation, %	7.6	8.5	6.5	5.8	7.1	6.0

Between generations: $F=1.86$; $P>0.05$; L.S.D.$=\pm 0.88$ gm.

Hen-house egg production

This study has clearly shown that egg production can be greatly improved in two generations by family selection and progeny testing even in small populations. From an average production of 180.2 eggs in the P_1 generation, there was an increase to 220.3 eggs in the F_2 and a high of 228.1 eggs in the F_4 generation. These differences, which are shown in table 15, were highly significant statistically.

As mentioned earlier, the P_1 population included four different strains originally bred under dissimilar environmental conditions. By selecting the phenotypically superior males and females from this group, the average production was raised only 4.1 eggs per bird housed in the ensuing generation, which indicates that even for a character of low heritability some improvement can be realized solely from phenotypic selection. The F_2 population represented chicks from partially progeny tested males (15.4 percent) and partially progeny tested females (5.1 percent), the other breeders being untested but selected on the basis of family performance. Through this method, it was possible to raise the average hen-house production to 220.3 eggs, for an increase over the previous generation of 36.0 eggs per bird housed. Using 25 to 35 percent fully tested and partially tested males and 15.9 to 22.5 percent fully tested and partially tested females, the F_3 average dropped to 210.0 eggs; rose to 228.1 eggs in the F_4; and dropped to 223.0 eggs in the F_5. The pattern of small changes in production from the F_2 to F_5 may indicate that with the very limited number of birds in each population, a plateau had been reached whereby no further genetic gain in this character can be realized with this method of selection.

In table 16 is shown the average egg production of the survivors for each generation. It can be seen that the increase or decrease from one generation to the next is closely correlated with the pattern of hen-house production, shown in table 15, and the hen-house livability, shown in table 4.

Pause in egg production and clutch size

A genetic pause in poultry is defined as the suspension of egg production for seven or more consecutive days. This should not be confused with non-

TABLE 15. Hen-house egg production*

CHARACTERISTIC	GENERATIONS					
	P_1	F_1	F_2	F_3	F_4	F_5
Number	313	173	150	150	155	163
Hen-house egg production	180.2	184.3	220.3	210.0	228.1	223.0
Standard deviation, eggs	71.4	73.6	59.9	57.1	57.6	70.7
Coefficient of variation, %	39.6	40.0	27.2	27.2	25.2	31.7

Between generations: $F=19.74$; $P<0.01$; L.S.D.$=\pm 13.73$ eggs; H.S.D.$=\pm 18.08$ eggs

*Based on first hatch of each generation. Chicks were hatched on March 3 (± 3 days) during this investigation.

TABLE 16. Average production of survivors (P_1-F_5)

Population*	Total eggs	No. birds	$\bar{x}$ production	Gain (over P_1)
P_1	50,500	248	203.6	—
F_1	16,286	77	211.5	+ 7.9
F_2	21,093	90	234.4	+30.8
F_3	29,573	133	222.4	+18.8
F_4	33,836	141	240.0	+36.4
F_5	34,867	148	235.6	+32.0

*(F_1-F_5) includes only the first hatch because of the similar hatching date of the P_1 generation.

production because of broodiness or molt. Clutch size is a measure of intensity of egg production and is calculated by dividing the number of clutches (groups of consecutive eggs) by the total egg production.

The average clutch sizes and pauses per generation are shown in table 4. From a low of 2.3 in the P_1 generation, the average clutch size was raised to a high of 3.2 eggs in the F_4 generation. The number of pauses per bird was also reduced from 1.8 in the P_1 generation to 1.3 in the F_5 generation. From these data, it would seem that these characters are associated with total egg production. When clutch size was increased and the number of pauses decreased there was a concomitant rise in the egg production.

Mortality

Because of its economic importance and low rate of heritability, mortality was measured at three different times for each generation. The first measurement was taken from hatching time to 6 weeks of age, the second from 6 to 12 weeks of age, and the third from time of housing to the end of the laying year—a total of thirteen 28-day intervals or 364 days.

As shown in table 4, there was no improvement in livability to 6 weeks of age until the F_5 generation, although in the F_4 generation it was approximately identical to that of the P_1 generation. A possible explanation for this is that the chicks of the P_1 population came from selected families of the different strains and consequently were bred for high livability. On the other hand, this low rate of mortality may be attributed to the isolation of these chicks in the brooders where conditions were such that they enhanced the possibility for maximum livability. In the ensuing generations, however, the inter-strain crosses brought about changes in the genotypes for resistance to the strains of diseases found in Hawaii and induced higher rates of mortality in the first three filial generations.

The picture at 12 weeks of age, however, was somewhat different. Except for the first filial generation, mortality to 12 weeks of age was very similar in the other selected generations. In the P_1 generation, the controls (Hawaii strain) had 1.1 percent mortality while the other four strains showed 4.6, 6.4, and 6.7 percent mortality. These data suggest that resist-

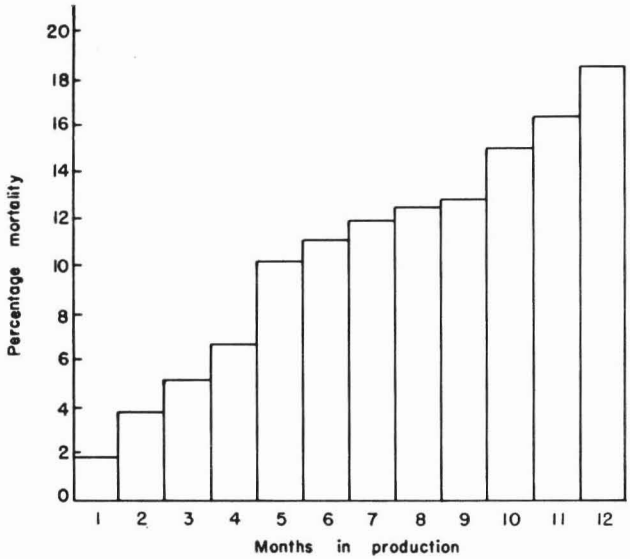

FIGURE 1. Cumulative mortality during laying year (P_1).

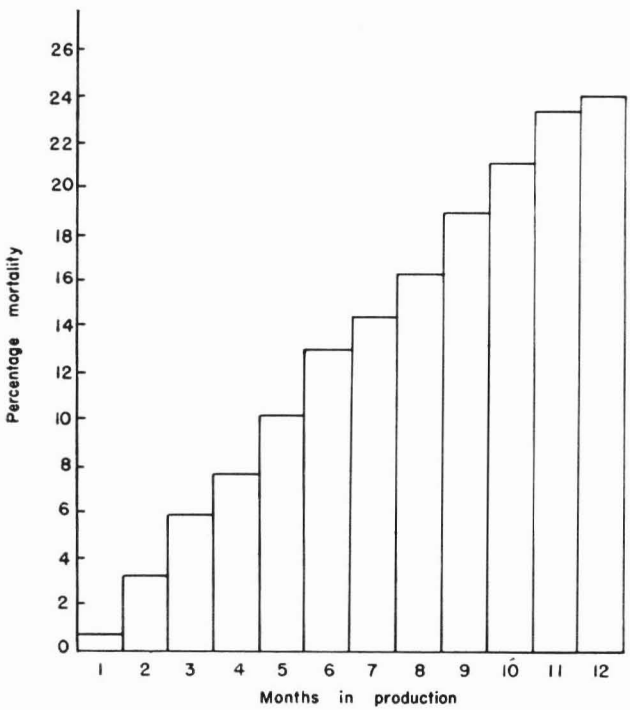

FIGURE 2. Cumulative mortality during laying year (F_1).

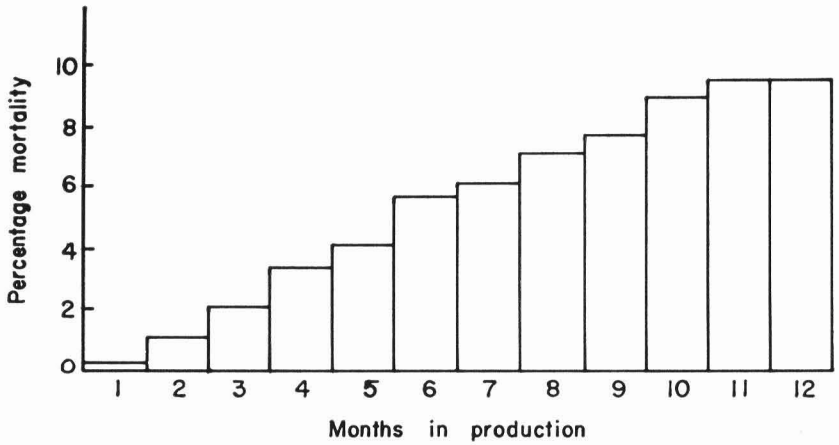

FIGURE 3. Cumulative mortality during laying year (F_2).

ance to disease was not as well developed in the imported strains as in the controls. However, it is fruitless to speculate in this manner because the extent to which the prevalence and concentration of disease organisms differ between the West Coast and Hawaii is not known. It is also not known whether the difference in the systems of management was responsible for the higher mortality; that is, strains bred for high livability and reared on litter and grass ranges may not have the same resistance when reared on wire.

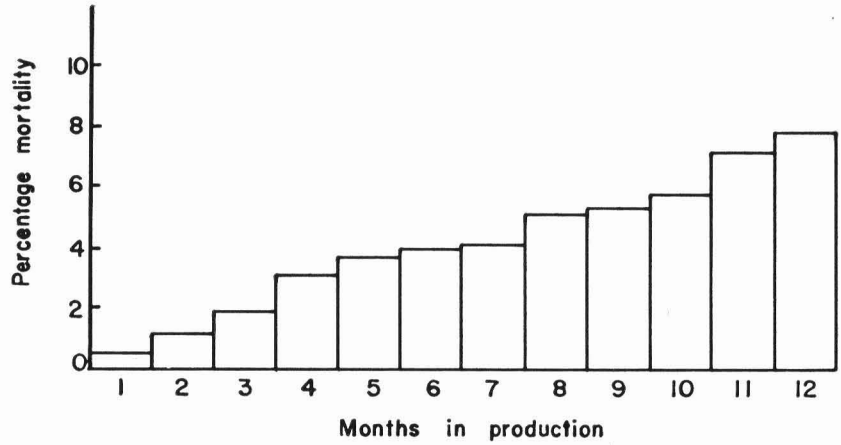

FIGURE 4. Cumulative mortality during laying year (F_3).

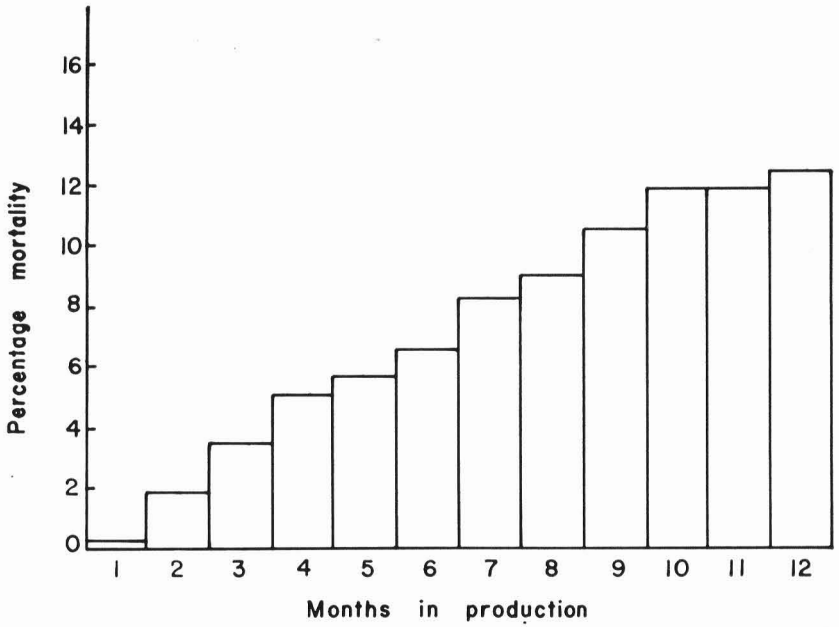

FIGURE 5. Cumulative mortality during laying year (F_4).

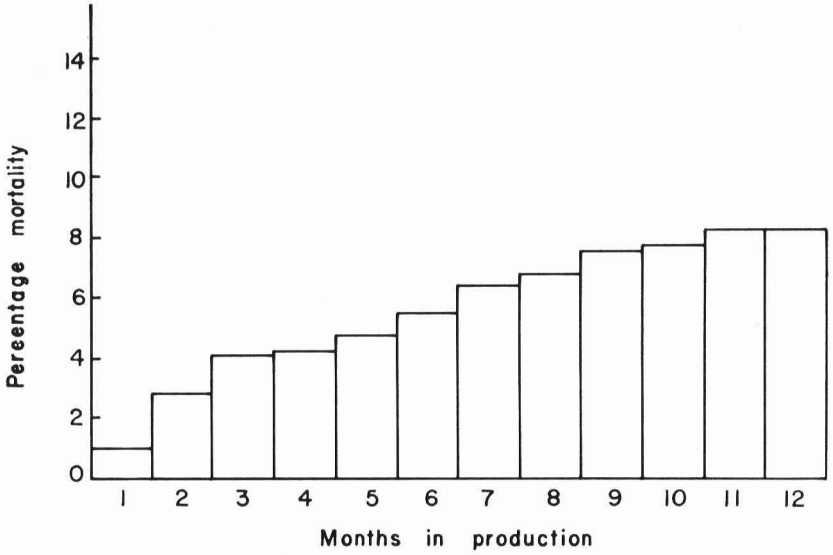

FIGURE 6. Cumulative mortality during laying year (F_5).

Hen-house mortality was closely associated with mortality to 12 weeks of age. Following 364 days of confinement production, the hen-house mortality was 19.0 percent for the P_1, 27.0 percent for the F_1, 7.2 percent for the F_2, 10.1 percent for the F_3, 9.0 percent for the F_4, and 8.4 percent for the F_5 generation. It was observed during the first three years of the study that many of the pullets were afflicted with neural lymphomatosis. During the next three years, however, not a single pullet was observed to have this manifestation of the leukosis complex. The greatest single cause of deaths during this study was visceral lymphomatosis.

In figures 1 to 6 are shown the cumulative mortality rates during the laying year for the P_1 to F_5 generations, respectively. It can be seen from these data that pullets are most susceptible to death during the first 6 months of egg production when more than 50 percent of the deaths occur. While the P_1, F_1, and F_2 generations showed a stair-step effect in mortality for the last 3 months of egg production, the F_3, F_4, and F_5 generations showed very low mortality during that period.

CONCLUSIONS

From the genetically variable parental stock, it was possible through family and progeny testing to improve characters of low heritabilities such as egg production and livability. As a result of the practice of using about 25 percent of partially or fully progeny tested males and 16 percent similarly tested females as breeders to produce the F_2, F_3, F_4, and F_5 generations, hen-house egg production was raised from 180.2 to 223.0 eggs. Actually, the F_1 generation was produced from the phenotypically superior males and females of the P_1 generation, and the gain in hen-house egg production was only 4.1 eggs for the F_1 generation. However, there was a gain of 36.0 eggs per bird housed in the F_2 generation when families were established through pedigree breeding and breeder candidates were selected on the basis of family performance. From the F_2 to F_5 generations, there was no definite pattern. Instead, there was a decrease, then an increase, and finally a decrease in the F_5 generation. This study has demonstrated that the method of selection exerted was ineffective in the improvement of egg production beyond a certain plateau when small populations are involved.

We have heard several comments by local poultrymen on the high standard of performance in egg production and the rather poor performance in livability of imported strains. In this study, for instance, the mortality of the imported strains was high as compared to the local strain. Through rigid family selection, it was possible to lower mortality at all ages in the succeeding generations. It is possible that the imported strains were susceptible to the local strains of disease organisms and that the system of wire-floor rearing may have contributed to the higher rate of mortality. Whatever the case may be, the fact remains that by rigid family and progeny testing, improvement was attained in this study. This would be a great

advantage to the local poultry economy because of the annual loss of investment and potential income attributed to high mortality.

For the characters of high heritability such as body weight and age at sexual maturity, improvement was obtained by phenotypic selection. In this study, body weights at all ages were significantly increased simply by selecting the larger sized males and females as breeders. Age at sexual maturity was also lowered by the selection of early maturing pullets.

This study demonstrated that appreciable improvement was made for such characters as livability, egg production, rate of growth, rate of feathering, and age at sexual maturity by planning a breeding program and exerting selection pressure in accordance with the heritability estimates for each character. Within our limited population, the improvement plateaus were more quickly reached for characters of low heritability than for those of high heritability. It would appear that to make additional gains in egg production and livability, a larger breeding population should be used.

SUMMARY

An attempt was made through pedigree breeding to develop from four genetically dissimilar strains of New Hampshires a superior strain adapted to the environmental conditions found in Hawaii. The results in this paper were obtained from five selected generations. Data were collected on fertility, hatchability, rate of growth, livability, perosis, rate of feathering, age at sexual maturity, egg weight, broodiness, number of pauses per bird, and clutch size.

It was found that significant improvement was made in such characters as egg production, livability, rate of growth, and rate of feathering. Most of the gains for characters of low heritability were attained during the F_2 generation, while further gains were made in subsequent generations via phenotypic selection only for characters of high heritability. No real reduction was made in the incidence of perosis, but this may have been due to the increased growth rate of the experimental birds. Whereas the number of pauses per bird was decreased and clutch size increased by the system of selection employed in this study, the incidence of broodiness was not successfully controlled.

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